

GENERIC RELATIONSHIPS IN THE
ANDROMEDEAE (ERICACEAE)

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THIS INVESTIGATION of generic relationships within the Andromedeae DC. was undertaken in connection with a monograph of *Lyonia* Nutt. (Judd, 1978), a genus that has often been confused with several related genera (especially *Pieris* D. Don) and that has been divided by some botanists into several smaller genera. The results of the phenetic and phylogenetic studies presented below have reaffirmed the generic distinctiveness of *Lyonia* and have clarified relationships among the related genera *Pieris*, *Arctericia* Coville, *Craibiodendron* W. W. Smith, *Agarista* D. Don, *Agauria* Hooker f., and *Leucothoë* D. Don.

The tribe Andromedeae (Ericaceae subfam. Vaccinioideae, see Stevens, 1970, 1971; Watson, 1965; Watson *et al.*, 1967) as circumscribed by Stevens (1970, 1971) comprises *Andromeda* L., *Oxydendrum* DC., *Chamaedaphne* Moench, *Craibiodendron* (including *Nuihonia* Dop), *Lyonia*, *Pieris*, *Arctericia*, *Agauria*, *Agarista*, *Zenobia* D. Don, *Leucothoë*, *Gaultheria* L. (including *Chiogenes* Salisb. and *Pernettya* Gaudich.), *Pernettyopsis* King & Gamble, *Tepuia* Camp, and *Diplycosia* Blume. Of these, *Andromeda*, *Oxydendrum*, and *Chamaedaphne* are considered to be isolated genera (see Stevens, 1970), while the remaining taxa fall into two general groups that are referred to by Stevens (1970) and here as the *Lyonia* group and the *Gaultheria* group.

The *Lyonia* group of genera tends to have biseriate-stalked multicellular hairs; paired bracteoles that are often at or near the base of the pedicel; slender, geniculate filaments; and short, rather broad anthers with an area of white disintegration tissue at the anther-filament junction. Staminal appendages, when present, are spurs, and the style is often swollen. The cells of the seed coat are usually much elongated with rather thin walls, the foliar stomata are anomocytic, and the leaf epidermis is often lignified. Bands of fibers are found in the secondary phloem of all genera, and the chromosome numbers, where known, are all $x = 12$. Stevens (1970) included *Lyonia*, *Craibiodendron*, *Pieris*, *Arctericia*, *Agauria*, and *Agarista* in this group. In contrast, the *Gaultheria* group, which includes *Leucothoë*, *Zenobia*, *Gaultheria*, *Pernettyopsis*, *Diplycosia*, and *Tepuia*, has multiseriate-stalked multicellular hairs, bracteoles that are usually paired and are often borne at the top of the pedicel, and filaments that are often stouter and never geniculate. In *Gaultheria*, *Leucothoë*, and *Zenobia* the anthers have awns and disintegration tissue; in the remaining genera, these characters are lacking, and the anther thecae are prolonged into terminal tubules. The cells of the seed coat are variable in shape and thickness, the foliar stomata are often paracytic or nearly so, and the leaf epidermis is not lignified. The type and arrangement of lignified cells

in the phloem is variable, but these cells do not occur in bands. Chromosome numbers, where known, are $x = 11, 12,$ and 13 (see Stevens, 1970). There are, however, many exceptions to the characters given above (see TABLE 1), and these groups (as pointed out by Stevens himself) are not so sharply defined. Most of the exceptions, which involve either *Agauria* and *Agarista* or *Pieris*, are discussed in more detail below.

Because *Lyonia* has often been fragmented into several genera (Small,

TABLE 1. Variation in selected morphological, anatomical, and cytological characters in *Lyonia*, *Pieris*, *Arctericia*, *Craibiodendron*, *Agarista*, *Agauria*, and *Leucothoe*.

CHARACTER	LYONIA SECT. ARSENOCOCCUS	LYONIA SECT. MARIA	LYONIA SECT. PIERIDOPSIS	LYONIA SECT. LYONIA	PIERIS SECT. PIERIS	PIERIS SECT. PHILLYREOIDES	PIERIS NANA (ARCTERICA)	CRAIBIODENDRON	AGARISTA	AGAURIA	LEUCOTHOË
PROSTRATE SHRUBS	-	-	-(+)	-	-	-	+	-	-	-	-
BANDS OF FIBERS IN PHLOEM (TWIG)	+	+	+	+	+	+	+	+	+	+	-
PITH TYPE (H = HETEROGENEOUS, E = HOMOGENEOUS, C = CALLUNA)	H	E	E	E	H	H(E)	E	E	C	CA, H	VAR.
PLANT EVERGREEN	-	-/+	-(+)	+	+	+	+	+	+	+	+/-
BUD SCALES	2	2-6(-8)	2	2	3-6	(2)3-4	≥3	2(-4)	2-4(-6)	>2	>2
SUPERPOSED BUDS	-	-	-	-	-	-	-	+	-	-	-
ELONGATED AT- TACHMENT OF BUD TO TWIG	-	-	-	-	-	+/-	-	+	-	-	+/-
ARRANGEMENT OF LEAVES (A = ALTERNATE, PV = PSEUDOVERTICILLATE, W = WHORLED)	A	A	A	A	A/PV	A/PV	W	A	A	A	A
NODE OFTEN 3 TRACES FROM 1 GAP	-	-	-	-	-	-	-	+	-	-	-
LEAVES REVOLUTE IN BUD	-	-	-	-	-	-	-	-	-/+	+	-
LEAVES LESS THAN 1.5 CM. LONG	-	-	-	-(+)	-	-	+	-	-(+)	-	-
LEAVES SERR- (UL)ATE	+	-	-	+/-	+	+	-	-	-(+)	-	+
DENSE LEAF VEIN RETIC- ULUM	-	-	-	-	-	-	-	-	+	+	-
INTRAMARGINAL LEAF VEIN	-	-/+	-	-	-	-	-	-	-	-	-
FREE LEAF FIBERS	-	-	-	-	-	-(+)	-	+	-	-	-
LEAF EPIDERMAL CELLS DIVIDED	-	-	-	-	-	-	-	-	+	-	-
LEAF HYPODER- MIS	-	-	-(+)	+(-)	-	-	-	+/-	-	+	-
LEAF EPIDERMIS LIGNIFIED	-(+)	-(+)	-(+)	+	-/+	-/+	+	+	+	+	-
LEAF MIDRIB BUNDLE BIFACIAL	+	+(-)	+	+	-	-(+)	-	+	-	-	-

TABLE 1. CONTINUED

CHARACTER	LYONIA SECT. ARSENOCOCCUS	LYONIA SECT. MARIA	LYONIA SECT. PIERIDOPSIS	LYONIA SECT. LYONIA	PIERIS SECT. PIERIS	PIERIS SECT. PHILLYREIODES	PIERIS NANA (ARCTERICA)	CRAIBIODENDRON	AGARISTA	AGAURIA	LEUCOTHOË
STOMATA ANOMOCYTTIC	+	+	+	+	+	+	+	+	+	+	-
ABAXIAL LEAF EPIDERMIS PAPILLOSE	-	-	-/+	-	-	-	-	-	-	+	-
ABAXIAL LEAF SURFACE DENSELY COVERED WITH UNICELLULAR HAIRS	-	-	-	-/+	-	-	-	-	-(+)	-	-
LONG-CELLED HAIRS	-	-	-	-	-/+	-	-	-	-	-	-/+
MULTISERIATE STALKED-GLANDULAR HAIRS	-	-	-	-	-	-	-	-	+	+	+
PELTATE SCALES	-	-	-	+	-	-	-	-	-	-	-
MULTICELLULAR SWOLLEN-HEADED HAIRS	+	+	+	+	-	-	-	-	-	-	-
INFLORESCENCE POSITION (A = AXILLARY, T = TERMINAL)	A	A	A	A	A/T	A	A	A	A	A	A
INFLORESCENCE TYPE (P = PANICULATE; RACEME OF FASCICLES, F = FASCICLE, R = RACEME, R' = RACEME WITH FLOWERS IN WHORLS OF 3, P = PANICLE)	'P'	F	R	F(R)	P(R)	R	'R'	P	R	R	R
INFLORESCENCE EXPOSED IN WINTER	-	-	-	-	+	+	+	-	-	-	+
BRACCTOLE POSITION (B = BASE, A = APEX)	B	B	B	CA, B	LO, 1/4 UP, 1/4	LO, 1/4 A	UP, 1/3	LO, 1/3	LO, 1/3	LO, 1/3	B TO A
RELATIONSHIP OF BRACCTOLES (A = ALT., O = OPP.)	O	O	O	O(A)	A(O)	A(O)	A	A/O	A/O	A/O	A/O
FLOWER ARTICULATE WITH PEDICEL	+	+	+	+(-)	+	+	+	+	+	+	+
AESTIVATION OF CALYX LOBES (V = VALVATE, I = IMBRICATE)	V (OPENING EARLY)	V (OPENING EARLY)	V	I	V (OPENING LATE)	V (OPENING LATE)	V	I	I	I	I
PROMINENT SEPAL FIBERS	-	-	-	-	+	+	+	-	-	-	-
ADAXIAL CALYX STOMATA	-	-	-	-	+	+(-)	-	-	-	-	-

TABLE 1. CONTINUED

CHARACTER	LYONIA SECT. ARSENOCOCCUS	LYONIA SECT. MARIA	LYONIA SECT. PIERIDOPSIS	LYONIA SECT. LYONIA	PIERIS SECT. PIERIS	PIERIS SECT. PHILLYREIODES	PIERIS NANA (ARCTERICA)	CRAIBIODENDRON	AGARISTA	AGAURIA	LEUCOTHOE
MEROSITY (COROLLA)	5	5	5	4-7(8)	5	5	5	5	5	5	5
COROLLA CAM- PANULATE	-	-	-	-(+)	-	-	-	+	-	-	-
COROLLA FLESHY	-	-	-	-(+)	-	-	-	+	-	-	-(+)
ABAXIAL COROLLA STOMATA	+	+	+	+	-	-	-	+	+	+	+
FILAMENTS GENICULATE	+	+	+	+	-	-(+)	-	+	+	+	-
STAMENS WITH SPURS	+	+	+/-	+/-	+	+	+	-	-	-	-
LOCATION OF SPURS (F = FILAMENT, J = ANTHER-FILAMENT JUNCTION)	F	F	F	F	J	J	J	NA	NA	NA	NA
DISINTEGRA- TION TISSUE ON SPURS	+	+	+	+	-	-	-	NA	NA	NA	NA
PUBESCENCE OF FILAMENTS (H = UNICELLULAR HAIRS, P = PAPILLAE OR SMALL PROJECT- IONS, S = SMOOTH)	H	H/P	H(P)	P	H	H(S)	P	P	H	H	H/P/S
ANTHERS WITH AWNS	-	-	-	-	-	-	-	-	-	-	+(-)
CAPSULE WITH THICKENED SUTURES	+	+	+(-)	+	-	-	-	-	-	-	-
PLACENTA POSI- TION (ON COLUMELLA OF CAPSULE: SA = SUBAPICAL, C = CENTRAL, B = BASAL, A = APIC- AL)	SA	C(±B)	SA(C)	SA	SA	C/±B	±B	SA	A(C)	B	A
SEED COAT CELLS (S = SHORT, L = LONG)	L	L	L	L	L	S	L	L	L	L	S
SEEDS WINGED (SL = SLIGHTLY)	-	-	-	-	-/2SL	-	-(SL)	1	-	-	- OR BULGING CELLS
CHROMOSOME NO. (N =)	12	12	12	12	12	?	?	?	12	?	11
GEOGRAPHY (N = NORTH AMERICA, W = WEST INDIES, E = EASTERN ASIA, N A = AFRICA, S = SOUTH AMERICA)		N W	E	W N	E N	N W E	E	E	S N	A	N E
NUMBER OF SPECIES	1	2	5	27	3	3	1	4?	34?	1	8

Note: rare or uncommon character states are given in parentheses.

1914, 1933; Britton & Brown, 1913) and confused with *Pieris* (Gray, 1878; Bentham & Hooker, 1876; De Candolle, 1839; D. Don, 1834; G. Don, 1834), I have attempted to reassess the generic limits within the *Lyonia* group. *Leucothoë* has also been included in this study for two reasons. First, *Agarista* has often been treated as a section of *Leucothoë* (De Candolle, 1839; Sleumer, 1959). Second, several species of *Pieris* and *Lyonia* have been considered by earlier botanists (De Candolle, 1839; Richard in Sagra, 1850) to be species of *Leucothoë*, and Lems found in a study of leaf anatomy in the Andromedeae (1964) that *Lyonia lucida* (here placed in *Lyonia* sect. MARIA) was quite similar to *Leucothoë axillaris* and *L. fontanesiana*.

PHENETIC STUDY

In the present study the six genera of the *Lyonia* group, along with *Leucothoë*, were compared on the basis of 50 morphological, anatomical, and cytological characters (TABLE 1). Each genus was considered to be an "Operational Taxonomic Unit" (OTU), except *Lyonia* and *Pieris*, which are quite variable and in which each section was treated as an independent OTU. To produce a matrix of character differences (TABLE 2), each OTU was compared with every other, and the number of characters for which each pair of taxa exhibits different states was recorded. When two or more states of a given character are common within a single OTU, then that OTU, when compared to a second OTU, was scored as similar in that character even if only one of the character states matched the character state(s) possessed by the second OTU. However, character states that were rare or uncommon within an OTU were not taken into consideration in the numerical analysis, although they are shown within parentheses in TABLE 1. A phenogram (FIGURE 1) was then constructed (using the matrix of character differences presented in TABLE 2) by calculating the character differences between the OTUs (or OTU clusters) and successively joining the most similar OTUs.

It is evident from this purely phenetic approach that one can recognize five groups of morphologically and anatomically similar OTUs among the taxa considered (see TABLE 2 and FIGURE 1). The OTUs within each group (above steplike line in TABLE 2) differ from each other by 3 to 8 (to 11) characters, while any two OTUs from different groups, when compared, differ in (12 to) 14 to 22 characters (below steplike line in TABLE 2). These groups correspond to (1) *Arctericia* and *Pieris*, (2) *Lyonia*, (3) *Craibiodendron*, (4) *Agarista* and *Agauria*, and (5) *Leucothoë* (see also FIGURE 1). The joining of *Arctericia* with *Pieris* (at 10.5 character differences) is in the "gray area" between OTUs that are clearly very closely related (differing in only a few characters) and those that are quite distinctive (differing in 14 or more characters). Thus, the separation of the *Arctericia-Pieris* group into two phenetic groups would also be consistent with the information presented in FIGURE 1 and TABLE 2. However,

TABLE 2. Matrix of character differences.

	ARCT	PIER	PHIL	PIED	ARSE	MARI	LYON	CRAI	AGAR	AGAU	LEUC
ARCT	—										
PIER	10	—									
PHIL	11	4	—								
PIED	19	18	17	—							
ARSE	21	16	16	3	—						
MARI	17	16	16	3	4	—					
LYON	19	20	20	7	8	6	—				
CRAI	21	22	22	17	19	16	14	—			
AGAR	19	16	16	14	16	14	15	14	—		
AGAU	20	18	16	16	18	16	16	16	5	—	
LEUC	19	13	13	18	18	18	20	19	12	15	—

ARCT = *Pieris nana* (*Arctica*); PIER = *Pieris* sect. PIERIS; PHIL = *Pieris* sect. PHILLYREOIDES; PIED = *Lyonia* sect. PIERIDOPSIS; ARSE = *Lyonia* sect. ARSENOCOCCUS; MARI = *Lyonia* sect. MARIA; LYON = *Lyonia* sect. LYONIA; CRAI = *Craibiodendron*; AGAR = *Agarista*; AGAU = *Agauria*; LEUC = *Leucothoë*.

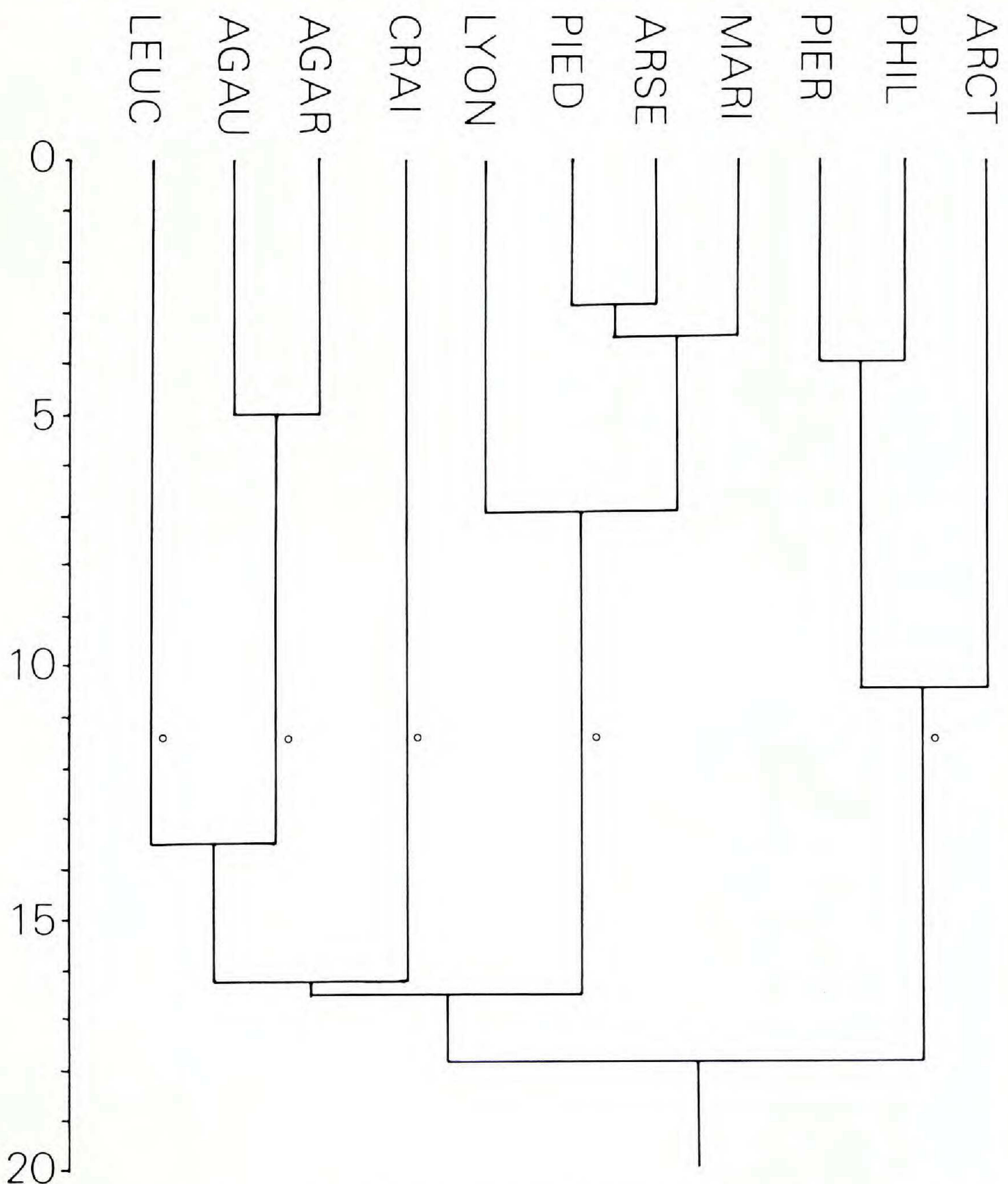


FIGURE 1. Phenogram based on character differences given in TABLE 2. ARCT = *Pieris nana* (*Arcteric*); PHIL = *Pieris* sect. PHILLYREOIDES; PIER = *Pieris* sect. PIERIS; MARI = *Lyonia* sect. MARIA; ARSE = *Lyonia* sect. ARSENOCOCCUS; PIED = *Lyonia* sect. PIERIDOPSIS; LYON = *Lyonia* sect. LYONIA; CRAI = *Craibiodendron*; AGAR = *Agarista*; AGAU = *Agauria*; LEUC = *Leucothoë*. An open circle (°) indicates each of the five phenetic groups discussed in the text.

because of the nature of the characters differentiating these two OTUs (see discussion below), they have been considered together.

Arcteric and *Pieris* are characterized by buds with 3 to 6 imbricate scales; leaves often pseudoverticillate; vascular bundle of the petiole or leaf midrib usually unifacial; fully mature flower buds that "overwinter" (i.e., inflorescences exposed for some time before flowering and with mei-

osis occurring in autumn); bracteoles variable in position but not at the base of the pedicel; calyx lobes stout, valvate in bud, and with prominent fiber strands associated with the vascular bundles (see Palser, 1951; Stevens, 1969); corollas lacking stomata on their abaxial surfaces; and filaments usually straight, with a pair of stout spurs at the anther-filament junction. In *Pieris* and *Arctericia*, the disintegration tissue does not extend onto the spurs. The monotypic *Arctericia* (*A. nana*) is phenetically much more similar to *Pieris* than to any other genus studied, differing only in having very small, entire-margined leaves that are in whorls of three, racemes in which the flowers are similarly whorled, twigs with a homogeneous pith, calyx lobes lacking stomata on their adaxial surfaces, and roughened-papillose filaments. It also differs in being a low, nearly prostrate, "heath-like" shrub. All of these characters except leaf arrangement vary infragenerically in one or more of the related genera. For example, the pith type is variable within *Lyonia*, *Pieris*, *Leucothoë*, and, to some extent, *Agauria*; stomata distribution on the calyx lobes differs in *Pieris*; and the filament indumentum varies within *Lyonia*, *Pieris*, and *Leucothoë*. From a phenetic standpoint it would appear that *Arctericia nana* does not possess sufficient morphological and anatomical distinctions to merit generic status; rather, it would be better treated as an isolated species within *Pieris* (perhaps in a section or subgenus by itself). Thus, in the remaining portion of the study, this species is referred to as *Pieris nana*. The relationships among the taxa included within *Pieris* will be discussed in more detail in a later paper.

Phenetically, *Lyonia* is a rather distinctive genus characterized by its buds with 2 scales (except in *L. mariana*), indumentum of biseriate-stalked multicellular hairs with more or less large, swollen heads, twigs usually with homogeneous pith, petiole or leaf midrib with a bifacial vascular bundle (except in *L. lucida*), inflorescences "overwintering" in the bud (i.e., not exposed for some time before flowering) with meiosis occurring in the spring, bracteoles usually opposite to subopposite and basal or nearly basal, calyx lobes lacking prominent fibers, and slender, geniculate filaments lacking appendages or having 2 spurs near the apex. In *Lyonia* the disintegration tissue of the anthers always extends onto the 2 rather slender spurs, when they are present, and in some taxa the filament spurs are actually completely disintegrated due to the development of this tissue. A final character unique to this genus is the distinctive thickened sutures of the capsule that in dehiscence often separate as a unit from the adjacent valves. (These distinctive sutures are present in all species except the rare eastern Asian *L. compta* and *L. chapaensis*.)

The recognition of any of the sections of *Lyonia* as genera is unwarranted because the number of distinguishing characters is relatively few. By comparison, there are many similarities between the sections; these distinguish *Lyonia* sensu lato from *Pieris*, *Craibiodendron*, *Leucothoë*, and other Andromedeae. Three genera — *Desmothamnus* Small, *Neopieris* Britton, and *Arsenococcus* Small — have been proposed as segregates from *Lyonia*.

Desmothamnus (Small, 1913, 1914, 1933), the only species of which is *D. (Lyonia) lucidus*, differs from the other species of *Lyonia* only in its leaves with an intramarginal vein, and in the unifacial vascular bundle of the petiole and leaf midrib. On various plants I have found occasional petioles that are slightly bifacial near the apex, and the venation type is quite variable among the remaining species of *Lyonia*, ranging from brochidodromous to eucamptodromous or nearly acrodromous (venation terminology *sensu* Hickey, 1973, and Dilcher, 1974). *Lyonia lucida* shares many characters with *L. mariana*, which was considered by Small (1914, 1933) to be the sole species comprising the genus *Neopieris*, although Britton and Brown (1913) had earlier placed both taxa in *Neopieris*. *Lyonia mariana* differs from other species of *Lyonia* only in its prominently urn-shaped capsules and deciduous calyx lobes, although the calyx lobes of *L. macrocalyx*, an eastern Asian species, are also occasionally deciduous. When considered together, *Lyonia mariana* and *L. lucida* differ consistently from other species of *Lyonia* only in their indumentum of multicellular, short-headed hairs and their buds with 2 to 6 (to 8) imbricate bud scales. To base genera on so few and such variable characters does not seem justifiable and certainly is not consistent with the magnitude of morphological discontinuities separating other commonly recognized genera in the Andromedeae.

Small (1913, 1914, 1933) treated *Lyonia ligustrina* as the genus *Arsenococcus*. (He included the morphologically distinctive populations of the Coastal Plain of the southeastern United States, which he considered to be *A. frondosa*, as a separate species.) Only its heterogeneous pith and paniculate inflorescences separate this taxon from the remaining species of *Lyonia*. Since the inflorescence type is variable within *Pieris* and, to some extent, in *Agarista*, since the pith type varies infragenerically in *Leucothoë*, *Pieris*, and slightly in *Agauria*, and since *Lyonia ligustrina* shows nearly all of the anatomical and morphological peculiarities of *Lyonia* listed above, it would be illogical to exclude this taxon. The Asian species (i.e., *Lyonia* sect. PIERIDOPSIS) are rather similar to *L. ligustrina* and help to ally this taxon even more closely with the remainder of the genus.

Although *Lyonia* sect. PIERIDOPSIS has often been referred to *Pieris*, this group differs from *Pieris* in its 2 large, imbricate bud scales; entire-margined and often deciduous leaves, which are not pseudoverticillate; indumentum of multicellular hairs with large, swollen heads; homogeneous pith; bifacial vascular bundle of the petiole; exclusively axillary and racemose inflorescences; opposite and basal bracteoles; lack of adaxial calyx stomata; presence of abaxial corolla stomata; geniculate filaments; spurs (when present) arising from the filament and with disintegration tissue; capsules with thickened sutures; calyx lobes lacking prominent fiber strands; and inflorescence "overwintering" within the bud. Species of *Lyonia* sect. PIERIDOPSIS were included in *Pieris* only because of the emphasis given to the presence of staminal spurs in *Lyonia ovalifolia*. It was thought that because this species (and several of its relatives) possessed this "key character" of *Pieris*, it must be placed in the genus (see

G. Don, 1834; De Candolle, 1839; Bentham & Hooker, 1876; Gray, 1878; J. D. Hooker, 1882; Brandis, 1911; Lecomte, 1930). In addition, some of the characters listed above were either unknown or misinterpreted by earlier botanists. The same reasoning was applied to *Lyonia lucida* and *L. mariana* (sect. MARIA), which have well-developed spurs near the apex of their filaments, and the result was the same (see Bentham & Hooker, 1876; Small, 1903). Actually, the spurs of *Lyonia ligustrina* (sect. ARSENOCOCCUS) are small, while those of several of the West Indian lyonias (sect. LYONIA) are quite well developed, but this fact was not known at the time. The spurs of *Lyonia* are, in reality, quite different from those of *Pieris*: in *Lyonia* they always arise from the filament and have a line of white disintegration tissue running along their upper margin; in *Pieris* they are at the anther-filament junction, and the disintegration tissue never extends onto the spurs. *Lyonia* sect. PIERIDOPSIS is best included in *Lyonia* because its taxa possess the complex of characters (given above) that characterize this genus. The section differs from the rest of the genus only in having racemose inflorescences.

Nieden zu (1890) considered *Lyonia* sect. LYONIA and *Chamaedaphne* to be congeneric, chiefly because they both have peltate scales. *Chamaedaphne* is in fact not very close to *Lyonia* sect. LYONIA, differing from it in its usually more or less paracytic stomata, apical bracteoles, stamens with straight filaments lacking appendages, anthers with terminal tubules, terminal inflorescences, unifacial leaf midrib bundle, capsules lacking thickened sutures, and presence of the yellow flavonol gossypetin (see Harborne & Williams, 1973). Even the leaf scales of the two groups are only superficially similar. The scales of *Lyonia* sect. LYONIA often have quite elongated stalks and fimbriate or irregular margins, while those of *Chamaedaphne* have very short stalks and nearly entire margins. The cells composing the scales of *Chamaedaphne* are also smaller and more regularly arranged.

Phenetically, *Craibiodendron* is an isolated genus characterized by its often superposed buds, which have 2 (to 4) bud scales and a rather elongated attachment to the twig; twigs with a homogeneous pith; bifacial vascular bundle of the petiole and leaf midrib; indumentum of biseriate-stalked, small-headed, multicellular hairs; axillary paniculate inflorescences with terminal flowers that "overwinter" within the bud; bracteoles usually positioned in the lower $\frac{1}{3}$ of the pedicel; clearly imbricate calyx lobes; more or less campanulate and carnose corollas; roughened-papillose and geniculate filaments that lack appendages; and large, thick-walled capsules bearing a few large seeds, each with a prominent unilateral wing.

Agauria and *Agarista* are characterized by buds with more than 2 bud scales; an indumentum of multiseriate-stalked, small-headed, multicellular hairs; leaves with a unifacial midrib bundle and a rather dense vein reticulum with all orders more or less equally prominent; bracteoles usually positioned in the lower $\frac{1}{3}$ of the pedicel; and geniculate filaments without appendages and covered with long unicellular hairs. In addition, the single species of *Agauria* and at least some species of *Agarista* have leaves that

are revolute in bud. The relationship between these two supposed genera and the characters by which they differ are discussed in detail by Stevens (1970), but it should be added that all the characters by which these two taxa differ (e.g., pith type, presence of papillae on abaxial leaf epidermis, placenta position, presence of a leaf hypodermis) are variable — infra-generically as well as infraspecifically — in at least one of the other major phenetic groups. *Agarista* and *Agauria* are phenetically very similar (TABLE 2 and FIGURE 1) and should be reunited into a single genus.

Leucothoë is distinguished by its indumentum of multiseriate-stalked hairs, unifacial leaf midrib bundle, leaves with an unligified epidermis and paracytic stomata, lack of fiber bands in the phloem of the twigs, imbricate calyx lobes, “overwintering” of nearly mature flower buds (i.e., inflorescences exposed in winter), straight filaments, anthers with awns (in some species), seeds with testa cells not elongated, and chromosome numbers (where known) of $x = 11$. This genus is distinct from the other genera (including *Agarista* and *Agauria*) in its awns, paracytic stomata, chromosome number, and lack of fiber bands in the phloem. *Leucothoë* also differs from all taxa studied (except *Pieris cubensis*, *P. swinhoei*, and *P. phillyreifolia*) in having seeds with the testa cells not strongly elongated. *Leucothoë* seems to be most similar to *Agarista/Agauria* and *Pieris*, but the magnitudes of the differences between these genera are such that to include either within *Leucothoë* would completely destroy the distinctive character combinations shown by these genera. The similarities of *Leucothoë* (in the *Gaultheria* group) with *Pieris* and *Agarista/Agauria* (in the *Lyonia* group) are likely due to the retention of many common primitive characters in these genera (but a few cases of parallel evolution may also be involved; see cladistic study). The relationships of *Leucothoë*, *Agarista*, and *Agauria* are discussed in detail by Stevens (1970).

CLADISTIC STUDY

The phenetic approach to the problem of generic limits discussed above is useful in suggesting phenetic affinities between groups, but much phylogenetic or cladistic information is lost or distorted by this method (see Hennig, 1966; Kavanaugh, 1972; Bremer & Wanntorp, 1978). Therefore, I have attempted to determine the phylogenetic or cladistic relationships (i.e., similarities due to synapomorphies) between and among the genera of the *Lyonia* group and *Leucothoë*. Taxa are grouped by their shared derived characters (synapomorphies) in accordance with the application of the criterion of parsimony. As in all cladistic methods, a great problem is to determine for each character which state is derived and which is ancestral (see Mayr, 1965, 1969; Ehrendorfer, 1976; Funk & Stuessy, 1978; and Stuessy, 1979, for other difficulties and for discussions concerning the application of cladistic methods).

Forty-five characters were used and assigned generalized (primitive, ancestral, or plesiomorphous) or specialized (advanced, derived, or apomorphic) states using the method of Wagner (1961, 1962, 1969). TABLE 3 lists these characters. Each taxon or OTU was scored 0 if generalized

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the *Lyonia* group of the Andromedeae.

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Habit	Trees to low shrubs	Prostrate, "heathlike"
B	Bands of fibers in the phloem	No	Yes
C	Pith	Homogeneous	a. Heterogeneous b. <i>Calluna</i> -type
D	Bud scales	2 small, opening to reveal several additional	a. Only 2 visible; large to small, imbricate b. 3, imbricate c. Many, small, imbricate, clearly spirally arranged
E	Number of buds/leaf axil	1	2, superposed
F	Attachment of bud to stem	Short	Elongated
G	Arrangement of leaves	Alternate, \pm equally spaced	a. \pm pseudover-ticillate b. In whorls of 3
H	Leaves deciduous	No	Yes
I	Vascular anatomy of node	1 trace from 1 gap	Often 3 traces from 1 gap
J	Arrangement of leaves in bud	Convolute	Revolute
K	Size of leaves	>1.5 cm.	<1.5 cm.
L	Leaf margin	Entire	Serrate or serrulate
M	Vein reticulum of leaf rather dense, all veins \pm equally prominent	No	Yes
N	Fiber strands in leaf mesophyll	No	Yes
O	Epidermal cells of leaf divided	No	Yes
P	Adaxial leaf hypodermis present	No	Yes
Q	Leaf epidermis	Not lignified	Lignified

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the *Lyonia* group of the Andromedeae (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
R	Petiole and leaf midrib vascular bundle	Unifacial	Bifacial
S	Stomata	Anomocytic	Paracytic
T	Abaxial leaf epidermis papillose	No	Yes
U	Abaxial leaf epidermis densely covered with unicellular hairs	No	Yes
V	Structure of stalk of multicellular hairs	Multiseriate	Biseriate
W	Peltate scales	Lacking	Present
X	Structure of head of multicellular hairs	Small	Large, swollen
Y	Head of multicellular hairs elongated	No	Yes
Z	Inflorescence type	Panicles (with terminal flowers)	a. Panicles (lacking terminal flowers) b. Racemes (lacking terminal flowers) c. Fascicles (lacking terminal flowers) d. Panicles (terminal, lacking terminal flowers) e. Racemes with flowers in whorls of 3 (lacking terminal flowers)
AA	Inflorescence "over-wintering" within bud	Yes	No
BB	Bracteole position	Tending to be positioned in lower $\frac{1}{3}$ of pedicel	a. Basal (or nearly so) b. Variable, near apex to within ca. lower $\frac{1}{3}$ of pedicel

TABLE 3. Characters used in phylogenetic study (Wagner method) of the genera of the *Lyonia* group of the Andromedeae (*continued*).

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
CC	Aestivation of calyx	Imbricate	Valvate
DD	Prominent fiber strands present in calyx lobes	No	Yes
EE	Adaxial calyx stomata present	No	Yes
FF	Number of flower parts	Usually 5-merous	4-, 6-, or 7-merous
GG	Corolla shape	Urceolate to cylindrical	± campanulate
HH	Thickness of corolla	Thin	Thick
II	Abaxial corolla stomata present	Yes	No
JJ	Filament shape	± straight	Geniculate
KK	Spurs present	No	Yes (but in some taxa probably secondarily lost)
LL	Spurs with disintegration tissue	No	Yes
MM	Indumentum of filaments	Unicellular hairs	a. Papillae b. Smooth
NN	Anthers with awns	No	Yes
OO	Capsule sutures	Unthickened	Thickened
PP	Placenta position	Apical or ± subapical	Basal to ± central
QQ	Cells of seed coat	± isodiametric	Strongly elongated
RR	Wings present	No	a. Yes; a single large wing on one side of seed b. Yes; a fimbriate wing around seed formed by outgrowths of individual cells c. Yes; a narrow wing on each side of seed
SS	Chromosome number	$x = 12$	$x = 11, 13, \text{etc.}$

and 1 if specialized for each of the characters. When two or more states of a given character are considered derived, each is given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). When both derived and generalized states of a character commonly occur within a single taxon, the abbreviation "var." for variable is recorded for this character. In the cladistic analysis this "var." condition is scored as a 1. If a character state occurs only rarely within an OTU, it is listed within parentheses after the predominating character state and is not considered in the cladistic analysis. (These two means of dealing with characters that vary within OTUs may introduce some slight distortion into the phylogenetic relationships determined.) All the taxa are listed in TABLE 4, with the character state values for each. The total divergence index of each taxon (or OTU) was determined by adding the individual character state values of each character. Then mutual groupings of derived characters between taxa were determined (by hand), and the taxa were arranged in sequence according to these groupings. They were plotted on a concentric graph (FIGURE 2), the branching points being determined by the mutual groupings of characters and the distance being determined by the divergence of each taxon. Thus, only the branching points and the evolutionary divergence values (i.e., the length of the lines) indicated by this figure are meaningful.

The Wagner method requires numerous assumptions concerning which is the derived and which is the generalized state of each character. Although these decisions were made after an extensive study of *Lyonia* and related genera, they are inevitably often rather subjective and thus introduce a major source of error.

Character states considered as derived for functional or ecological reasons include: leaves deciduous; habit low, heathlike, shrubby; adaxial calyx stomata present; "overwintering" of nearly mature flower buds; buds with two large, imbricate scales; anther filaments geniculate; staminal spurs present; sepals with prominent fiber strands; seeds variously winged; capsules with thickened sutures; and leaves less than ca. 1.5 cm. long. The role of function in the evolutionary interpretation of comparative data is considerable (see discussion in Simpson, 1961; Davis & Heywood, 1963; Mayr, 1969; Stebbins, 1974), especially when the functional/ecological analysis of homologous characters is carried out across several related taxonomic groups (i.e., out-group comparison). Functionally specialized characters found in one or a few taxonomic groups (and not in the out-groups) are considered derived.

Deciduous leaves occur in groups that are otherwise (e.g., in anatomy, floral morphology) very different, and it seems likely that they have evolved independently where this character is of adaptive value. For example, the deciduous *Lyonia ovalifolia* var. *elliptica* occurs in cool to warm-temperate areas of Japan, while the related semi-evergreen var. *rubrovenia*¹ is a plant of the warm and moist forests of Hainan. Both

¹ *Lyonia ovalifolia* (Wallich) Drude var. *rubrovenia* (Merrill) Judd, comb. nov. (*Pieris rubrovenia* Merrill, Philip. Jour. Sci. 23: 256. 1923).

TABLE 4. Character states used in the construction of the Wagner Tree.

Character	<u>Lyonia</u> sect. <u>Arsenococcus</u>	<u>Lyonia</u> sect. <u>Pieridopsis</u>	<u>Lyonia</u> sect. <u>Maria</u>	<u>Lyonia</u> sect. <u>Lyonia</u>	<u>Pieris</u> sect. <u>Pieris</u>	<u>Pieris</u> sect. <u>Phillyreoides</u>	<u>Pieris</u> nana (<u>Arctericca</u>)	<u>Craibiodendron</u>	<u>Agarista</u>	<u>Agauria</u>	<u>Leucothoë</u>
A	0	0(1)	0	0	0	0	1	0	0	0	0
B	1	1	1	1	1	1	1	1	1	1	0
C	la	0	0	0	la	la(0)	0	0	lb	la	var.
D	la	la	var. (c)	la	0	0	lb	la	0	0	0
E	0	0	0	0	0	0	0	1	0	0	0
F	0	0	0	0	0	var.	0	1	0	0	var.
G	0	0	0	0	la	la	lb	0	0	0	0
H	1	1(0)	var.	0	0	0	0	0	0	0	var.
I	0	0	0	0	0	0	0	1	0	0	0
J	0	0	0	0	0	0	0	0	0(1)	1	0
K	0	0	0	0(1)	0	0	1	0	0	0	0
L	1	0	0	var.	1	1	0	0	0(1)	0	1
M	0	0	0	0	0	0	0	0	1	1	0
N	0	0	0	0	0	0(1)	0	1	0	0	0
O	0	0	0	0(1?)	0	0	0	0	1	0	0
P	0	0(1)	0	1(0)	0	0	0	var.	0(1)	1	0
Q	0(1)	0(1)	0(1)	1	var.	var.	1	1	1	1	0
R	1	1	1(0)	1	0	0(1)	0	1	0	0	0
S	0	0	0	0	0	0	0	0	0	0	1
T	0	var.	0	0	0	0	0	0	0	1	0
U	0	0	0	var.	0	0	0	0	0(1)	0	0
V	1	1	1	1	1	1	1	1	0	0	0
W	0	0	0	1	0	0	0	0	0	0	0
X	1	1	1	1	0	0	0	0	0	0	0
Y	1	1	0	0	0	0	0	0	0	0	0
Z	la	lb	lc	lc	ld	lb	le	0	lb	lb	lb
AA	0	0	0	0	1	1	1	0	0	0	1
BB	la	la	la	la(0)	lb	lb	lb	0	0	0	lb
CC	1	1	1	0	1	1	1	0	0	0	0
DD	0	0	0	0	1	1	1	0	0	0	0
EE	0	0	0	0	1	1(0)	0	0	0	0	0
FF	0	0	0	var.	0	0	0	0	0	0	0
GG	0	0	0	0(1)	0	0	0	1	0	0	0
HH	0	0	0	0(1)	0	0	0	1	0	0	0(1)
II	0	0	0	0	1	1	1	0	0	0	0
JJ	1	1	1	1	0	1(0)	0	1	1	1	0
KK	1	1(0)	1	1(0)	1	1	1	0	0	0	0
LL	1	1	1	1	0	0	0	NA	NA	NA	NA
MM	0	0	var. (a)	la	0	0(lb)	la	la	0	0	var. (a,b)
NN	0	0	0	0	0	0	0	0	0	0	1(0)
OO	1	1(0)	1	1	0	0	0	0	0	0	0
PP	0	0(1)	1	0	0	1	1	0	0(1)	1	0
QQ	1	1	1	1	1	0	1	1	1	1	0
RR	0	0	0	0	var. (c)	0	0(lc)	la	0	0	lb(0)
SS	0	0	0	0	0	0?	0?	0?	0	0?	1
TOTAL	17	16	16	19	16	17	17	16	8	11	12

Leucothoë racemosa and *Lyonia ligustrina* have chartaceous, deciduous leaves and occur in North America at latitudes much farther north than any of the evergreen species within their respective genera. In the Ericaceae, the generalized condition of the leaves seems to be coriaceous

and persistent, but cold-adapted species in a wide range of very distantly related genera have evolved deciduous and much thinner ones. Deciduous leaves occur in some or all of the species of *Arctostaphylos* Niedz., *Enkianthus* Lour., *Oxydendrum*, *Lyonia*, *Leucothoe*, *Vaccinium* L., *Gaylussacia* H.B.K., *Elliottia* Muhl. ex Ell., and *Rhododendron* L. Similarly, the "heathlike" habit and reduced leaves of *Pieris nana* are probably of adaptive significance in the cold-temperate and alpine situations in which it occurs.

Several interesting developmental inflorescence patterns occur within the Andromedeae. These were first studied by K. Lems (1962), who pointed out that the Ericaceae (which probably originated in a tropical or subtropical climate; see Bell & Burchill, 1955; Wulff, 1946) have a slow morphogenetic cycle, and that such genera as *Pieris*, *Leucothoe*, and *Chamaedaphne*, upon encountering summer-winter climates, have evolved unusual adaptations, including the "overwintering" of dormant and exposed flowers. Other genera, such as *Lyonia*, *Craibiodendron*, *Zenobia*, and *Andromeda*, evolved often large, protective bud scales (modified leaves) to enclose the embryonic inflorescence. The complete development of the inflorescence in the year preceding flowering may allow the plant with this developmental pattern to produce a large, many-flowered inflorescence and still bloom extremely early in the season, since the entire inflorescence and floral structure are already formed, and the flowers have only to open and the stigmas to become receptive for pollination (see Lems, 1962). Several other character states are functionally correlated with this condition, since, if the flower buds are exposed during the winter, the calyx must be modified (i.e., be lengthened to enclose the corolla tightly or be thickened and lignified to protect the internal floral parts). Conversely, the two large, imbricate bud scales of *Lyonia* or *Craibiodendron* provide winter protection for the partially formed inflorescence developing within them, while in *Pieris* or *Leucothoe* such enlarged bud scales are not necessary. The presence of adaxial calyx stomata (and possibly the lack of abaxial corolla stomata) in *Pieris* is also probably correlated with the method of inflorescence development in this genus.

Although winged seeds have arisen independently several times and are probably of adaptive value in dispersal, they are not found in most genera of the Ericaceae. In some species of *Leucothoe* (and *Rhododendron* and *Enkianthus*), cells around the edge of the seed have balloonlike processes that collectively form a fimbriate wing, while in *Pieris floribunda* the seed is flattened and there are small lateral wings of undifferentiated cells (see Stevens, 1969). The very distinctive seeds of *Craibiodendron* have a single large wing (also of cells no different from those covering the body of the seed) on one side. The seeds of this genus are the largest in the *Lyonia* group, and the large wing may enable them to be carried farther by the wind than would otherwise be possible. There is probably less selective pressure for winged seeds in genera with very small, light seeds, such as *Lyonia* or *Agarista*. Other modifications

include the wing of seeds of *Pterospora* Nutt., which is greatly swollen and is produced at the chalazal end of the seed, and the tail of seeds of *Ledum* L., *Menziesia* J. E. Sm., and especially *Rhododendron* sect. VIREYA (see Stevens, 1969). Some species of *Lyonia* sect. LYONIA also have tails at each end of the seed, although they are much smaller. All of these diverse modifications are considered to be evolutionary specializations.

Capsules with prominently thickened (and lignified) sutures that in dehiscence often separate as a unit from the adjacent valves occur only in *Lyonia*, although slightly thickened sutures can be seen in *Enkianthus* and *Oxydendrum* (in which they never separate as a distinct unit). These structures are probably important in seed dispersal, since the capsules are held erect and are persistent, letting the seeds sift out of the cracks between the valves and the sutures over a long period of time. Thus, these thickened and separating sutures are considered to be derived from the typical nonthickened ericaceous capsule-suture, leading to an increased efficiency of the "salt-shaker" mechanism of seed dispersal by wind.

Staminal spurs occur in a scattering of genera throughout the Ericaceae; for example, in the Vaccinioideae they are found in *Andromeda*, *Pieris*, and *Lyonia* of the Andromedeae, in such genera as *Vaccinium*, *Dimorphanthera* F. Mueller, and *Psammisia* Klotzsch of the Vaccinieae, in *Cassiope* D. Don and *Harrimanella* Cov. of the Cassiopeae, and in such genera as *Arctostaphylos* Adanson and *Arbutus* L. of the Arbuteae. They are also common in the Ericoideae and the Monotropeoideae. The spurs of these various groups are morphologically diverse — for example, flattened in the Ericoideae, robust in many Vaccinieae and Arbuteae, and slender and fragile in *Lyonia*. Their position varies (they can arise from either the filament as in *Lyonia*, the anther-filament junction as in *Pieris*, or the anther connective tissue beyond the point of union of anther and filament as in many Vaccinieae), and they can be paired structures, which is the usual condition, or single structures, as in *Anthopteropsis* A. C. Sm. and some species of *Dimorphanthera* (Stevens, 1969; pers. obs.). It thus seems likely that spurs may have some adaptive significance, probably related to the pollination mechanism, and have evolved independently (and secondarily become lost and regained) in many different groups within the family. This argument is reinforced by the fact that species with exerted stamens (and thus with a very different pollination mechanism) are usually devoid of spurs (see Artopoulos, 1903; Matthews & Knox, 1926; and Stevens, 1971). The slender, geniculate filaments and/or spurs of the *Lyonia* group probably act as an obstacle to the proboscis of pollinators, causing pollen to be sifted out of the anthers, and are thus functionally important in the pollination biology of these species. It is interesting that taxa with geniculate filaments, with the exception of *Pieris phillyreifolia*, tend to lack stout spurs. Therefore, it is possible that the presence of one structure (geniculate filaments) makes the second (spurs) functionally redundant, and it is of interest that in *Lyonia*, which has both geniculate filaments and

spurs, the spurs are usually rather small and fragile and are possibly nonfunctional. Spurs may have been acquired early in the evolution of the *Lyonia* group (as evidenced by their presence in both *Lyonia* and *Pieris*) but were subsequently lost in many taxa that developed geniculate filaments (*Craibiodendron*, *Agarista*, and *Agauria*).

The interrelationships of the various inflorescence types and the probable primitive condition will be discussed in detail in a later paper, but the inflorescence of *Craibiodendron*, which possesses terminal flowers, is likely primitive within the Andromedeae (see Weberling, 1965).

Several additional character states probably also developed through selective pressures relating to their functions, but the nature of these interactions is less well known. These include superposed (supernumerary) buds; the presence of a dense covering of unicellular hairs on the abaxial leaf surface; the presence of peltate scales; 4-, 6-, or 7-merous flowers; campanulate and/or carnose corollas; and pseudovercillate or whorled leaves. Superposed buds occur only in *Craibiodendron*, where both buds produce paniculate inflorescences. The dense layer of unicellular hairs on the abaxial leaf surface of many species of *Lyonia* sect. LYONIA and of *Agarista mexicana* var. *pinetorum*² may function in retarding water loss. The lepidote indumentum of *Lyonia* sect. LYONIA possibly protects the growing shoots from water loss, extremes of temperature, or over-heating due to solar radiation. The campanulate and carnose corollas of *Craibiodendron* are probably important in the pollination biology of that genus. Fleshy (or carnose) corollas occur also in some species of *Rhododendron*, a few species of *Lyonia* sect. LYONIA, and several tropical genera of Vaccinieae. The increased (or decreased) number of flower parts observed in some lyonias (especially *Lyonia* sect. LYONIA) may be a means of increasing (or decreasing) the number of seeds produced, or it may be the result of selection for larger (or smaller) flowers. Finally, pseudovercillate leaves, which occur in such diverse genera as *Rhododendron*, *Agapetes* D. Don ex G. Don, and *Pieris*, probably affect the photosynthetic capability of the plant (see Horn, 1975).

The following character states were considered derived at least in part because they are uncommon either within the *Lyonia* group or in the Ericaceae as a whole (i.e., they are found in only a single taxon or in only a few phenetic groups): bud scales imbricate, 2 large or 3; buds superposed; attachment of bud to twig elongate; habit low, "heathlike"; fiber bands present in phloem of older twigs; leaves pseudovercillate or whorled; node of three traces from one gap; leaves deciduous; leaves less than 1.5 cm. long; leaves revolute in bud; leaf epidermal cells divided;

² This taxon and its relatives have usually been included in *Leucothoë* and were referred to by Sleumer (1959) as *Leucothoë* sect. *Agastia*; see also Stevens (1970). The following new combinations are made here: ***Agarista mexicana*** (Hemsley) Judd var. ***mexicana***, comb. nov. (*Andromeda mexicana* Hemsley, Biol. Centr.-Am. Bot. 2: 282. 1881); ***Agarista mexicana*** (Hemsley) Judd var. ***pinetorum*** (Standley & Williams) Judd, comb. nov. (*Leucothoë pinetorum* Standley & Williams, Ceiba 3: 54. 1952); and ***Agarista populifolia*** (Lam.) Judd, comb. nov. (*Andromeda populifolia* Lam. Encycl. Méth. Bot. 1: 159. 1783).

leaf hypodermis present; all veins of leaf (except midvein) more or less equally prominent and densely reticulate; stomata paracytic; abaxial leaf epidermis papillose or densely covered with unicellular hairs; indumentum of peltate scales; multicellular hairs with elongated heads; multicellular hairs with more or less large, swollen heads; bracteoles strictly basal or tending to be near apex of pedicel; flowers 4-, 6-, or 7-merous; corolla more or less campanulate, fleshy; abaxial corolla stomata absent; staminal spurs with disintegration tissue; anthers with awns; capsules with thickened sutures; placentae basal; and chromosome numbers other than $x = 12$.

It is difficult to defend uncommonness as a criterion of advancement when only the within-group distribution of a character is considered, since the distribution of character states depends upon the phylogeny of the group and where within the sequence a particular character changes. Thus, this criterion was used in conjunction with other lines of evidence and then only after a comprehensive examination of the pattern of variation within the Andromedeae and Vaccinioideae.

Finally, several character states are rather arbitrarily considered to be derived because they seem to be correlated with one or more of the derived character states described above. They are: vascular bundle of petiole and leaf midrib bifacial; leaves with free fibers in the mesophyll; leaves serrulate or serrate; multicellular hairs with biseriate stalks; calyx lobes valvate in bud; filaments papillose; seed coat cells strongly elongated.

The Wagner Tree (FIGURE 2) resulting from the above procedure depicts the same five groups indicated by the phenetic analysis. These five groups are listed below along with the derived character states commonly present in or characteristic of each group. The characters listed for each group include some that are unique to and constant or nearly constant within the group, indicated by a double asterisk (**); some that are unique to the group but are only found in some species, indicated by a single asterisk (*); some that are not unique to the group but are constant within it, indicated by a double dagger (‡); and some that are neither unique to nor constant within the group, indicated by a single dagger (†).

The *Pieris* group is designated by the following derived characters: B (fiber bands in phloem)‡, Q (leaf epidermis often lignified)†, V (multicellular hairs usually with biseriate stalks)‡, AA ("overwintering" of nearly mature flower buds)‡, BB^b (bracteoles often positioned near apex of pedicel)‡, CC (calyx lobes valvate)‡, DD (sepals with prominent fiber strands)**, II (abaxial corolla stomata lacking)**, KK (spurs present)‡, and QQ (seed coat cells elongated, lost in *Pieris* sect. PHILLYREOIDES)†.

The genus *Lyonia* is characterized by the following derived characters: B (fiber bands in phloem)‡, D^a (buds usually with 2 imbricate scales)†, R (vascular bundle of petiole bifacial)‡, V (multicellular hairs with biseriate stalks)‡, X (multicellular hairs with large, swollen heads)**,

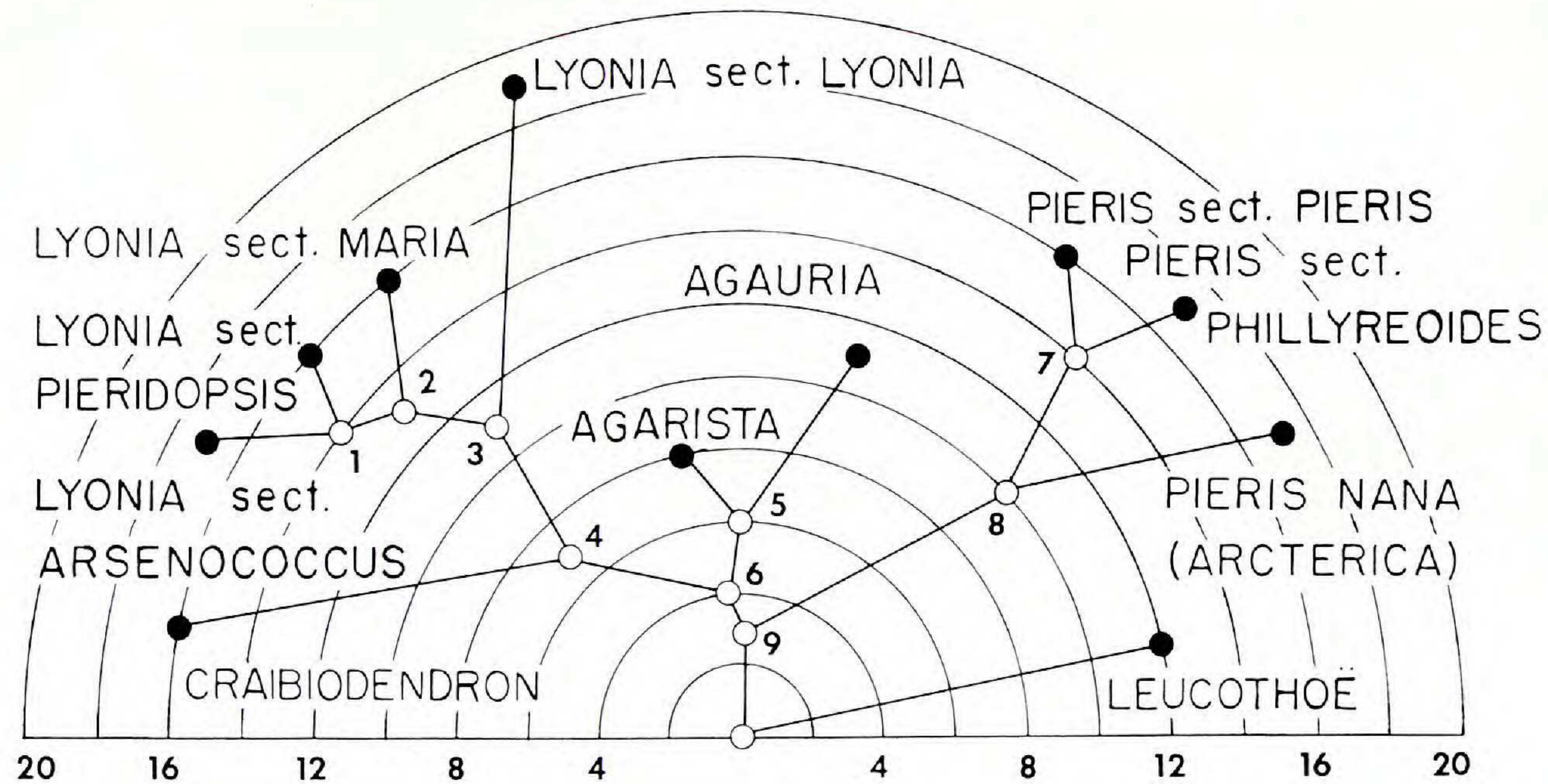


FIGURE 2. Wagner Tree for the genera of the *Lyonia* group of the Andromedeae (also including *Leucothoë*): present day taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles). Derived character states for each taxon: *Craibiodendron* — B, D^a, E, F, I, N, P, Q, R, V, GG, HH, JJ, MM^a, QQ, RR^a; *Lyonia* sect. ARSENOCOCCUS — B, C^a, D^a, H, L, R, V, X, Y, Z^a, BB^a, CC, JJ, KK, LL, OO, QQ; *Lyonia* sect. PIERIDOPSIS — B, D^a, H, R, T, V, X, Y, Z^b, BB^a, CC, JJ, KK, LL, OO, QQ; *Lyonia* sect. MARIA — B, D^c, H, R, V, X, Z^c, BB^a, CC, JJ, KK, LL, MM^a, OO, PP, QQ; *Lyonia* sect. LYONIA — B, D^a, L, P, Q, R, U, V, W, X, Z^c, BB^a, FF, JJ, KK, LL, MM^a, OO, QQ; *Agarista* — B, C^b, M, O, Q, Z^b, JJ, QQ; *Agauria* — B, C^a, J, M, P, Q, T, Z^b, JJ, PP, QQ; *Pieris* sect. PIERIS — B, C^a, G^a, L, Q, V, Z^d, AA, BB^b, CC, DD, EE, II, KK, QQ, RR^b; *Pieris* sect. PHILLYREOIDES — B, C^a, F, G^a, L, Q, V, Z^b, AA, BB^b, CC, DD, EE, II, JJ, KK, PP; *Pieris* (*Arcteric*) *nana* — A, B, D^b, G^b, K, Q, V, Z^e, AA, BB^b, CC, DD, II, KK, MM^a, PP, QQ; *Leucothoë* — C^{a,b}, F, H, L, S, Z^b, AA, BB^b, MM^{a,b}, NN, RR^b, SS. For hypothetical ancestors: 1 — B, D^a, H, R, V, X, Y, BB^a, CC, JJ, KK, LL, OO, QQ; 2 — B, D^a, H, R, V, X, BB^a, CC, JJ, KK, LL, OO, QQ; 3 — B, D^a, R, V, X, BB^a, JJ, KK, LL, OO, QQ; 4 — B, D^a, R, V, JJ, KK, QQ; 5 — B, M, Q, Z^b, JJ, QQ; 6 — B, JJ, KK, QQ; 7 — B, C^a, G^a, L, Q, V, AA, BB^b, CC, DD, EE, II, KK, QQ; 8 — B, Q, V, AA, BB^b, CC, DD, II, KK, QQ; 9 — B, KK, QQ.

BB^a (bracteoles basal or nearly so)***, JJ (filaments geniculate)‡, KK (spurs present)‡, LL (spurs with disintegration tissue)***, OO (capsules with strongly thickened sutures)***, and QQ (seed coat cells very elongated)‡.

Craibiodendron possesses the following derived characters: B (fiber bands in phloem)‡, D^a (buds with 2 imbricate scales)‡, E (superposed buds)***, F (buds with elongated attachment to twig)‡, I (node often with three traces from one gap)*, N (fibers in leaf mesophyll)*, P (leaves often with hypodermis)†, Q (leaf epidermis lignified)‡, R (vascular bundle of petiole bifacial)‡, V (multicellular hairs with biseriate stalks)‡, GG and HH (corolla more or less campanulate and fleshy)***, JJ (filaments geniculate)‡, MM^a (filaments roughened-papillose)‡, QQ (seed coat cells very elongated)‡, and RR^a (seeds with single large wing on one side)**.

The *Agarista-Agauria* group shares the following derived characters: B (fiber bands in phloem)‡, M (veins of leaves densely reticulate with all veins more or less equally prominent)***, Q (leaf epidermis lignified)‡, Z^b (racemes, terminal flowers lacking)‡, JJ (filaments geniculate)‡, and QQ (seed coat cells very elongated)‡.

The genus *Leucothoë* is distinguished by: C^{a,b} (some species with heterogeneous or *Calluna*-type (i.e., with small cells around the outside and larger cells in the center) pith; see Stevens, 1970)†, F (buds of some species with elongated attachment to twig)†, H (some species with deciduous leaves)†, L (leaves serrate)‡, S (stomata paracytic)***, Z^b (racemes, terminal flowers lacking)‡, AA (inflorescences exposed for some time before flowering)‡, BB^b (bracteoles at apex of pedicel in some species)†, MM^{a,b} (some species with papillose filaments, others smooth)†, NN (several species with awns)*, RR^b (some species with winged seeds, derived from balloonlike outgrowths of individual cells)*, and SS (chromosome number, where known, of $x = 11$)**.

Several examples of the loss of a derived character within a group are revealed. One is the probable loss of spurs in *Craibiodendron*, *Agauria*, *Agarista*, and a few species of *Lyonia*; a second is the loss (in all but an occasional leaf) of the bifacial midrib bundle in *Lyonia lucida*. *Pieris cubensis*, *P. phillyreifolia*, and *P. swinhoei* (*Pieris* sect. PHILLYREOIDES) have lost the elongated seed coat cells that probably characterized their ancestors and that are still present in *P. japonica*, *P. formosa*, *P. floribunda* (*Pieris* sect. PIERIS) and *P. nana*. The lack of epidermal lignification in the leaves of many individuals of *Lyonia ligustrina* (sect. ARSENOCOCCUS), *L. lucida* and *L. mariana* (sect. MARIA), and in *Lyonia* sect. PIERIDOPSIS is probably a reversal of the derived condition (epidermis lignified), which is the common condition in the *Lyonia* group of genera.

A few examples of parallel evolution of characters are also evident within this group. Some of the more interesting are: the presence of biseriate-stalked multicellular hairs in *Pieris* and *Lyonia/Craibiodendron*; the heterogeneous pith of *Lyonia* sect. ARSENOCOCCUS, *Pieris*, and *Agauria*; the serrate or serrulate leaves of many species of *Lyonia* sects. LYONIA

and ARSENOCOCCUS, *Pieris*, and *Agarista populifolia*; the papillae that densely cover the abaxial leaf surface of *Agauria* and a few species of *Lyonia* sect. PIERIDOPSIS; the dense covering of unicellular hairs on the abaxial leaf surface of *Agarista mexicana* var. *pinetorum* and many species of *Lyonia* sect. LYONIA; the basal placentae of *Agauria* and *Pieris* sect. PHILLYREOIDES, and the often nearly basal placentae of *Lyonia* sect. MARIA; the papillose or roughened filaments of *Craibiodendron*, *Lyonia* sect. LYONIA, *Lyonia lucida*, and *Pieris nana* (in most cases probably due to the loss of long unicellular hairs), and the geniculate filaments of *Pieris phillyreifolia* and *Lyonia/Craibiodendron/Agarista/Agauria*. Another example, although not evident from this phylogenetic analysis, is the presence in a few species of small, extremely revolute leaves in both *Agarista* and *Lyonia* sect. LYONIA. There are also many examples of parallel evolution between *Leucothoë* and the genera of the *Lyonia* group. These can be easily determined by scanning TABLE 4 for any "supposed" shared derived characters. If the function of these characters were more clearly understood, or if the evolutionary history of the group were better known, this situation could probably be readily explained.

The results of the cladistic analysis (see FIGURE 2) also indicate a relationship between *Craibiodendron*, *Agauria* and *Agarista*, and *Lyonia*. These taxa all have geniculate filaments and very elongated seed coat cells. All have abaxial corolla stomata, and embryonic inflorescences that "overwinter" within protective bud scales; all lack prominent fiber strands in the calyx lobes. In addition, *Craibiodendron* and *Lyonia* both have buds with two imbricate bud scales and a bifacial leaf midrib bundle. These four genera form an evolutionary line perhaps weakly distinct from *Pieris*, which has inflorescences that develop in the year preceding flowering and are thus exposed during the winter, prominent fiber strands in the calyx, corollas that lack stomata on the abaxial surface, and usually straight filaments. All five genera have fiber bands in the phloem of the branches. Thus, the results do seem to support the hypothesis that *Lyonia*, *Craibiodendron*, *Agarista*, *Agauria*, and *Pieris* form a related group of genera. This *Lyonia* group is best characterized by the presence of fiber bands in the phloem, but other useful characters include the elongated seed coat cells, the geniculate filaments and/or spurs, and a tendency toward epidermal lignification.

The phylogenetic isolation of *Leucothoë* is demonstrated by this cladistic study, although it was not evident from the phenetic investigation (using an almost identical set of characters) due to the many cases of parallel evolution of characters between the two groups. This parallel evolution is possibly the result of similar selective pressures on groups with quite similar genetic backgrounds. The cladistic distinctiveness of *Leucothoë* is especially expressed by the presence of awns (in several species) and paracytic stomata, by a chromosome number of $x = 11$, and by the lack of fiber bands in the phloem and elongated testa cells. FIGURE 2 supports the phenetic study in its close grouping of *Agarista* and *Agauria*, two taxa that should undoubtedly be considered as a single

genus. The low level of advancement of these two taxa made them appear rather more similar to *Leucothoë* in the phenetic study than the phylogenetic analysis has shown them to be because both *Agarista/Agauria* and *Leucothoë* have retained several primitive character states (that have often been variously modified in related genera). For example, both groups have two small bud scales that soon open (as the bud develops) to reveal several additional scales (D); alternate and more or less equally spaced leaves (G) with a unifacial midrib vascular bundle (R); multi-seriate-stalked multicellular hairs (U) with small, round, glandular heads (X and Y); imbricate calyx lobes (CC); urceolate to cylindrical, 5-merous, thin corollas (FF, GG, and HH); abaxial corolla stomata (II); and capsules with unthickened sutures (OO). In addition, both lack adaxial corolla stomata (EE) and filament spurs (KK). Thus, much of their phenetic similarity (see FIGURE 1) is due to many shared primitive characteristics. As in the phenetic treatment, *Pieris nana* is shown to be most closely related to the species of *Pieris* sects. PIERIS and PHILLYREOIDES and could be treated as an isolated and monotypic subgroup of this genus.

CONCLUDING COMMENTS

It seems most in accordance with the results of both phenetic and phylogenetic analyses to recognize four monophyletic groups within the *Lyonia* group of genera, one leading to *Agauria* and *Agarista*, one to *Craibiodendron*, one to *Lyonia*, and one to *Pieris* (including *Pieris nana*). In addition, the fundamental separation between the *Lyonia* and *Gaultheria* groups is supported if *Leucothoë* can be taken as typical of the latter.

Even if the relationships illustrated in FIGURE 2 were completely accurate, it would not remove all the arbitrary aspects of the determination of generic limits. However, it would allow one to be more consistent in the application of characters and to estimate the taxonomic "usefulness" of any given character within the group in question. In the *Lyonia* group of the Andromedaceae, it seems least arbitrary and most informative of evolutionary relationships to consider each of the four major evolutionary lines at the generic level, with their ultimate branches as either sections or subgenera (see Hall & Clements, 1923).

ACKNOWLEDGMENTS

This study is based on a portion of a dissertation, "A Monograph of *Lyonia* (Ericaceae)," which was submitted in partial fulfillment of the Ph.D. degree at Harvard University. I wish to express my sincere appreciation to Dr. Carroll E. Wood, Jr., for his guidance and encouragement during the course of this investigation. It was thought best to publish the present study of generic relationships within the Andromedaceae separately from the remaining portions of the dissertation. Drs. Carroll E. Wood, Peter F. Stevens, and Norton G. Miller provided many useful

comments and helpful suggestions concerning the manuscript. I wish especially to thank Dr. Peter F. Stevens for his thoughtful suggestions concerning taxonomic problems in the Ericaceae. Thanks also go to Michael Donoghue, Christopher Campbell, and Philip Cantino for their questions and comments.

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